

NOTES ON SEMPER'S LARVÆ FOUND IN THE VICINITY OF SETO

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ONE PLATE AND FIVE TEXT-FIGURES

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INTRODUCTION

The so-called Semper's larvæ of the Zoantharia belong to the most striking plankton organisms peculiar to the tropical waters. Since their discovery by Semper in 1867, they have been recorded from various spots of the tropical and subtropical seas of the world. Their appearance, the attitude during swimming and the internal structure have been described thoroughly by previous authors, notably by van Beneden (1898), Heath (1906), Senna (1907), Conklin (1908) and Carlgren (1924). The metamorphosis has been traced by Cary (1904) and Menon (1914, 1926).

There are two distinct types of Semper's larvæ thus far known, both of which have external appearances quite unlike any other coelenterate larva. The one named *Zoanthella* has a larger and more elongated body, and reminds one somewhat of a tiny slug, while the other, *Zoanthina*, is smaller, stocky and not unlike a trochophore. What is common to both the types is a band of strong cilia; but this band is longitudinal and stretches along the ventral line in *Zoanthella*, whereas in *Zoanthina* it is transverse and circumscribes the body at some distance from the oral end. According to Menon (1926) who reared these larvæ found in the Indian seas through metamorphosis, a small species of *Zoanthella* developed into a *Sphenopus*, while a larger one which is probably *Zoanthella galapagoensis* Heath became a *Palythoa*; one of the two species of *Zoanthina* metamorphosed into a *Zoanthus*, while the other became an adult which was very likely an *Isaurus*.

Both of these types of larvæ are found in plankton in the neighbor-

hood of our Seto Marine Biological Laboratory, though they are by no means very common. *Zoanthella* was recognized first in the summer of 1921 by the late Prof. I. Ikeda, when he and myself spent some days in a house in the village of Seto, and were making a preliminary survey of the fauna in that vicinity. *Zoanthina* was found in the plankton during next summer, while we were directing the laboratory course of students in the newly established laboratory; but it was unknown to us then. However, Mr. Y. Miyashita who was then a student of the Tokyo Imperial University and happened to be in the laboratory, brought home some of the specimens, sectioned them, and was able to identify them as *Zoanthina*.

During my short stay in the laboratory in the middle of last December, both the types of the larvæ appeared rather abundantly in plankton, mingled with other organisms evidently tropical in origin, such as floating Ceriantharia larvæ, *Doliolum* spp., *Sagitta* spp., pteropods, gigantic Auriculariæ, Tornariæ, and various polychæte and molluscan larvæ. Thus altogether more than a dozen specimens of *Zoanthina* and 4 of *Zoanthella* were obtained. The largest specimen of *Zoanthina* bore a lateral bud. Besides, I found a curious larva which appeared like a *Zoanthina*, but had two distinct ciliary belts instead of one, and was colored purplish red instead of the usual brownish color of *Zoanthina*. Sections of this specimen afterwards have revealed that this is a larva belonging to this group, but it has a very striking characteristic to be described later. I propose to call this *Trochanthina bicincta* n. g., n. sp.

Zoanthella and *Zoanthina* have been studied and described sufficiently, so that I shall confine myself to brief description of the forms found at Seto. Moreover, I shall not attempt to identify the specimens before me with the described species, since most of these are based on a single specimen, and it is very probable, at least in some cases, that the alleged specific characters represent only the distinctions found in different developmental stages. In consulting literature necessary for this study, I am indebted to the kindness of Professors A. Oka, H. Ohshima and T. Uchida.

Zoanthella

The larger specimens of this larva measure some 8.5 mm. in length and about 1.5 mm. in thickness, in the fully stretched state. The body is elongated and roughly cylindrical in form, but with different thickness

in the two extremities. At the more slender end, is found the mouth opening, while the other end is blunt and appears somewhat inflated. The band of locomotory cilia runs parallel to the longitudinal axis along the ventral side of the body. It begins close to the mouth at the anterior end, and terminates at the point about one-third the length of the body from the aboral end. The ciliary band is depressed somewhat from the general surface so as to produce a longitudinal furrow. The band is double in the posterior half of its length; this feature is more apparent in sections as will be pointed out later. The cilia adhere into a membrane in the basal parts, but the free ends are separate and beautifully iridescent.

In cross-sections the outline of the body of this larva is largely circular in the thicker aboral portion, with but a small incision formed by the ciliary band; but it appears reniform in the more slender oral portion, owing to the proportionally large part occupied by the band. The general surface of the body is also ciliated; but the cilia are much smaller as compared with the locomotory cilia.

The ground color of the body is pale yellowish, and marked with dark reticular patches which produce a somewhat marmorated appearance much like Senna's sketch of *Z. galapagoensis* (1907, fig. 13). The aboral end is almost uniformly dark.

When swimming, the larva stretches the body and keeps the aboral end upward, and takes a vertical position (text-fig. 1, A). The ciliary band beats something like the comb-plates of a ctenophore, and propels the body which advances describing a clockwise whorl when viewed from the oral side. When disturbed, the cilia suddenly cease to beat, and the larva shrinks and curls up around the ciliary band (text-fig. 1,

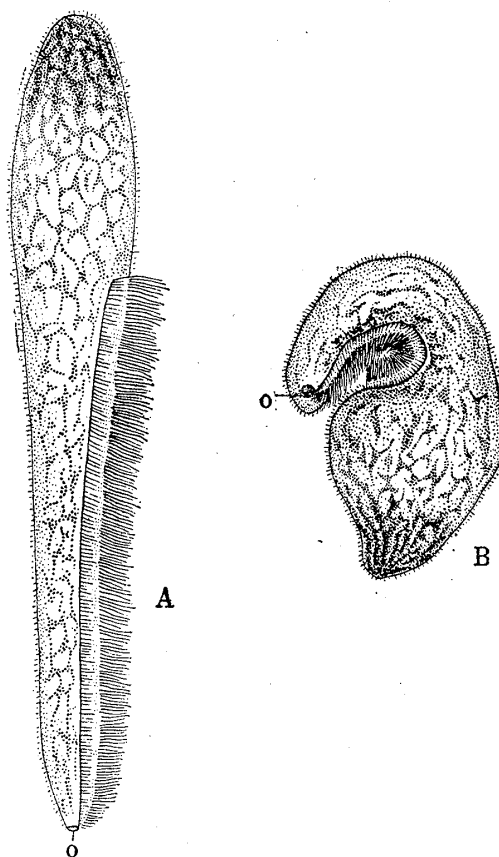


Fig. 1.—*Zoanthella*. Drawn from life. $\times 10$.
A. Larva in swimming and wholly expanded state. B. The same specimen in contracted state. o, oral aperture.

B) and falls to the bottom. In such a state, the appearance of the larva recalls that of a tiny slug.

The internal structure, as well as the histology of the individual parts of *Zoanthella*, has been described thoroughly by Senna and Conklin, so that any further comments seem hardly necessary. Only it may be pointed out that, in the posterior half of its length, the ciliary band is parted into two longitudinal halves by a ridge of non-ciliated epidermis inserted between them, as is noted also by both Heath and Conklin. The epidermis of the general surface of the body is penetrated by pigment cells with very long processes. The nematocysts are of two different types. One of them is small and elongated, and occurs more commonly in the superficial part of the epidermis, while the other type which is more rarely found, is very large and ovoid, and occurs in the deeper part. In some specimens most of the larger type of nematocyst are apparently in the course of the degenerative change and appear uniformly dark and irregular in outline. The endoderm contains some symbiotic zooxanthellæ, but in a smaller quantity than in *Zoanthina*. At the base of a short stretch of endoderm inserted between the ventral mesentery and the adjoining secondary mesentery, is found a group of rather thick longitudinal muscle-fibers, which evidently serve for making the larva curl up when it is disturbed.

Zoanthina

The second type of Semper's larvæ appears not unlike a trochophore in the contracted state. But in swimming attitude, it is elongate and cylindrical, tapering slightly toward either end. The band of locomotory cilia circumscribes the body in the region about 1/4 of the length from the oral end. The general surface is ciliated, but the cilia are incomparably weaker than the locomotory cilia. When swimming, the ciliary band beats from the aboral to the oral direction something like the comb-plates of a ctenophore. By this movement the larva is propelled in water with the aboral end ahead, describing a clockwise whorl (text-fig. 2, A). If disturbed, the larva contracts to such an extent that its length hardly exceeds its diameter, and becomes trochophore-like; in this state twelve meridional ridges become apparent on the surface (text-fig. 2, B). The body is dark brown through the presence of symbiotic zooxanthellæ in the endoderm; the ciliary covering of the body appears whitish by light-reflection. The aboral

end has a tint of dark green on the general dark brown ground. The internal structure needs hard any description, since it conforms very well with previous authors' accounts. All of the specimens are in the 12-mesentery stage, being provided with 6 pairs of primary and 6 pairs of secondary mesenteries.

The histology is nearly the same as in *Zoanthella*. As the only difference, it may be pointed out that the smaller nematocysts are less numerous, while the zooxanthellæ in the endoderm are decidedly more abundant.

The largest specimen of *Zoanthina* which measures some 8 mm. in length and 2 mm. in diameter in the fully stretched state, has a lateral bud (text-fig. 3). As shown in the figure, this bud is attached beneath the ciliary ring and has its own ciliary ring; it is about 1.5 mm. long and 0.5 mm. in diameter. The color of the specimen is somewhat deeper than the other specimens, being chocolate-brown, except the bud which is much lighter. The specimen was fixed and sectioned (Plate 4, fig. 1); but owing to an awkward orientation, it has become somewhat difficult to study its internal structure. However, as far as could be ascertained by the reconstructing method, it is also in the 12-mesentery stage. The bud is located in the bilateral plane of the mother individual, and is provided with a mouth-opening, gullet and about 6 mesenteries in the portion distal to the ciliary ring, while the proximal portion which is connected with the mother's body, is practically empty, being covered only with the direct continuation of the epidermis and its endodermal lining from the maternal body. The longer (bilateral) axis of the gullet of the bud coincides with that of the mother's gullet.

In this specimen, the mesogloea is thicker than in the other specimens and has more cells imbedded in it. The endoderm shows enormous thickening on either side of the mesentery. Besides, there is a

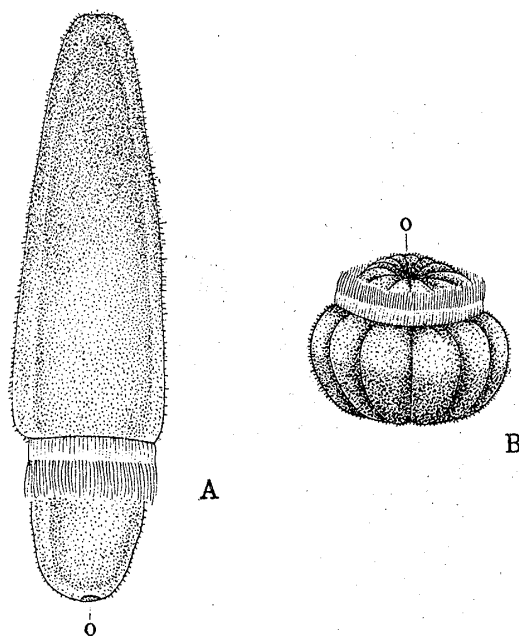


Fig. 2.—*Zoanthina*. Drawn from life. $\times 10$.
A. Larva in swimming and wholly expanded state. B. The same specimen in contracted state.

large pillar of endoderm which stands on the aboral wall of the body, as noted also by Carlgren in one of his specimens. The endoderm of various parts of the body shows a great quantity of inclusions which stain with eosin very vividly.

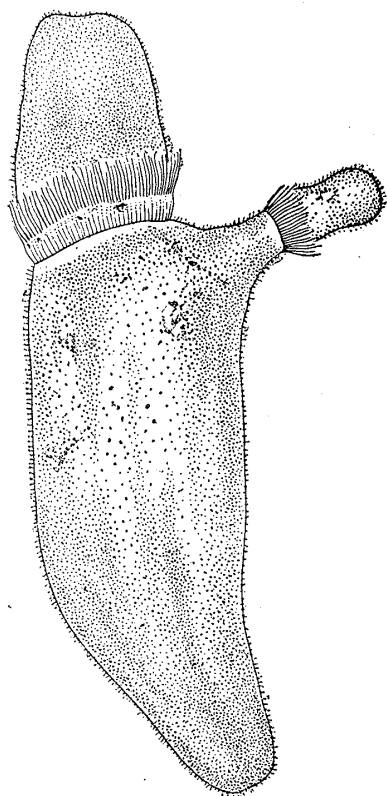


Fig. 3.—*Zoanthina*. The largest specimen with a lateral bud. Drawn from life. $\times 10$.

The budding of Semper's larvæ has never been reported. Van Beneden records that he found four very young larvæ in the gastric cavity of a specimen of *Zoanthina nationalis* van Beneden which he sectioned. The origin of these encased larvæ is utterly unknown; moreover, no similar observation has been reported since. It is difficult to tell whether my observation on budding has anything to do with the encasement of the young larvæ recorded by van Beneden.

Among the actiniæ the budding in the larval stage is noted in *Actinia equina* by Weill (1926); the encasement of embryos in the maternal body was observed in two specimens of actinian larvæ by Carlgren (1925). In this case there is no doubt that the embryos were produced by pædogenesis, since one of the larvæ contained large ova in some mesenteries.

Trochanthina bicincta n. g., n. sp.

This curious larva was found in the same swarm of plankton which yielded the above two kinds of Semper's larvæ. The novelty of the appearance of the larva, with bright purplish-red color and two distinct ciliary belts, struck me at the first glance, in spite of the smallness of the body which measured ca 1 mm. in length and 0.8 mm. in diameter. However, I had suspicion that it would possibly be a trochophore, before I sectioned it. The attitude while alive was not very different from *Zoanthina*; but it swam about more actively than *Zoanthina*, and did not shrink much if it was disturbed. Fig. 4, A represents the appearance of this larva in the living state, while fig. 4, B is a sketch of the same specimen after fixation. Sections have revealed

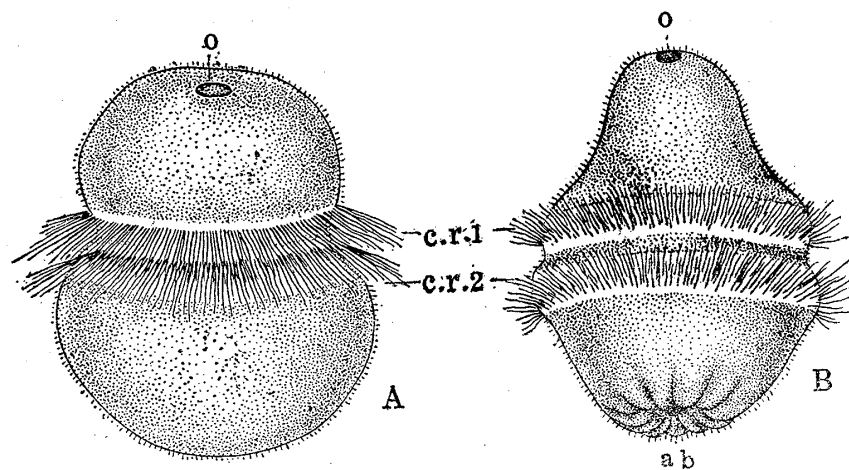


Fig. 4.—*Trochanthina bicincta*. $\times 40$. A. In living state. B. After fixation. *ab*, aboral opening; *c.r. 1.*, *c.r. 2.*, ciliary rings; *o*, oral aperture.

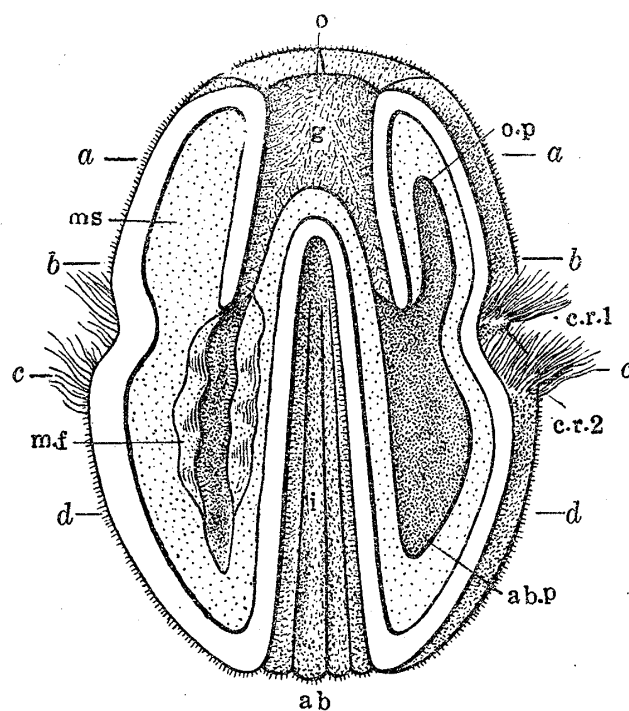


Fig. 5.—Diagrammatic figure showing the structure of *Trochanthina bicincta*. *aa-dd*, the levels from which the sections in Plate 4, figs. 2-5 have been derived; *ab*, aboral opening; *ab. p.*, aboral pocket of gastric cavity; *c.r. 1.*, *c.r. 2.*, ciliary rings; *g*, gullet; *i*, aboral invagination; *m.f.*, mesenteric filament; *ms*, mesentery; *o*, oral aperture; *o.p.*, oral pocket of gastric cavity.

beyond any doubt that the larva belongs to the same type as Semper's larvæ, and probably represents a developmental stage of some kind of Zoantharia. As may be seen in the diagrammatic figure (text-fig. 5) and also in the photomicrographs in Plate 4, the larva is provided with an opening on either pole of the main axis of the trochophore-like body. The one which is on the more slender pole, is the mouth opening and leads into the gullet. The gullet is compressed in one plane in the external half of its length (fig. 2, *g*), and is marked with a sulcus at one end of the longer diameter (*s*). In the internal half, the gullet is widened and appears circular in the cross-section (fig. 3, *g*). The aboral opening leads into a long tubal invagination whose blind end reaches even beyond the aboral extremity of the gullet and lies in the cavity of the latter (text-fig. 5, *i*; Pl. 4, figs. 3-5, *i*). The wall of the invagination goes over directly into the epidermis of the general surface of the body at the base of the invagination, and is thrown into some longitudinal foldings. The endoderm covers the other side of the invagination entirely, as it lines the outer surface of the gullet. There are 6 complete mesenteries, without any primordium of micromesentery between them. The mesenteries stretch between the gullet and the body wall, as well as between the basal portion of the aboral invagination and the body wall, so that the gastric cavity forms two sets of pockets, one around the gullet (oral gastric pockets, text-fig. 5, *o. p*), and the other around the base of the aboral invagination (aboral gastric pockets, *ab. p*). In the region between these two sets of coelic pockets, i.e. around the distal portion of the invagination, the mesenteries are interrupted and divided each into external and internal halves which are connected with the body wall and the wall of the aboral invagination respectively. The free margins of both of these halves are lined with the mesenteric filaments of the same type as those found in the other larvæ (Pl. 4, fig. 4, *m. f*).

The histology of each part of the body of this larva requires no detailed description, since it is very much the same as in the other larvæ. The epidermis is ciliated, as also the internal wall of the aboral invagination. The latter is furnished with an abundance of the smaller type of nematocyst, but with very few gland cells. Some longitudinal muscle-fibers occur at the base of the wall close to the mesogloea. The part of the epidermis which carries the locomotory cilia is quite similar to the corresponding part of the other larvæ. The endoderm harbors a great quantity of zooxanthellæ.

As to the function of the aboral invagination, it is difficult to form

any idea, my observations in the living state being regrettably short of answering this question. Some of the specimens of *Zoanthina* examined after fixation, show an aboral invagination somewhat like that of this form. However, such an invagination, which has been formed by shrinkage of the specimen, never appears to such an extent as that of *Trochanthina*. Moreover, the relation of the aboral invagination with the mesenteries of this larva is quite characteristic. These features, coupled with the duplicity of the ciliary belt, seem to warrant the establishment of a new genus for this larva.

The larva described by Cary (1904) apparently shows some resemblance to the present form, especially in having two ciliary rings instead of one. But, since he does not give any description of the internal structure, we can hardly make any further comparison of the two larvæ.

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EXPLANATION OF PLATE 4.

Fig. 1. Photomicrograph of a section cut parallel to the bilateral plane of the specimen of *Zoanthina* with a lateral bud. $\times 20$. *B.* bud. *c.r.*, ciliary ring of the mother. *c.r'*., the same of the bud. *g.*, gut. *o.*, oral aperture.

Figs. 2-5. Photomicrographs of transverse sections of *Trochantina bicincta*. $\times 90$.

2. Section through the external portion of the gullet on the level *a-a* in Text-fig. 5, showing 6 mesenteries and 6 oral pockets of the gastric cavity. *g.*, gullet. *g.c.*, gastric cavity. *s.*, sulcus.
3. Section through the aboral extremity of the gullet on the level *t-b* in Text-fig. 5. *g.*, gullet. *i.*, aboral invagination near its oral extremity.
4. Section through the region of a ciliary ring on the level *c-c* in Text-fig. 5. *c.r.*, ciliary ring. *i.*, aboral invagination. *m.f.*, mesenteric filaments. Note that the mesenteries are divided into external and internal halves each of which is provided with a mesenteric filament on the margin.
5. Section through the region of the aboral pockets of gastric cavity on the level *d-d* in Text-fig. 5. *g.c.*, gastric cavity. *i.*, aboral invagination.

SEMPER'S LARVAE
TAKU KOMAI

PLATE 4

